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THE RELATION OF THE LICHEN TO ITS ALGAL HOST
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In a paper recently published, the lichen was defined as a fungus which lives during all or part of its life in parasitic relation with an algal host and also sustains a relationship with an organic or an inorganic substratum. For those who do not care to read this lengthy paper¹, we may summarize briefly regarding the algal hosts of lichens, their growing together with lichens free in nature, cultures of lichens with and without the algal hosts, cultures of algal hosts separately, the growth of lichen hosts and other algae on media with and without light and CO₂., breathing pores and other means of aëration of the algal hosts of lichens, lichens as carriers of food to their algal hosts, hypotheses regarding the relation of the lichen to its algal host, and the relation of the lichen and its host to the substratum.

We have many times found the algal hosts of certain lichens growing near lichens but not parasitized by them, and have also more than once seen the spores of lichens germinating and attacking free algæ. Schwendener also found free *Nostoc* colonies, others penetrated by a few lichen hyphæ, and others parasitized by fully developed *Collema*s, all growing together, and recorded about the same relationship between a half dozen other lichens and their algal hosts. The list of lichens that are known to grow beside non-parasitized algæ of the host species in nature could be greatly extended, had we space to consider the observations of de Bary, Kny, Bornet, Zukal, Cunningham, Ward, Peirce, Williams, Nylander, Fuisting, Stahl, Hedlund and others. It is also well known that a considerable number of lichens live for months or

¹Fink, Bruce. The nature and classification of lichens—II.

The lichen and its algal host. *Mycologia* 5:97—166, 1913.

years in nature outside the relationship with algæ, and all these facts prove the fallacy of all theories of dual organism, mutualism, consortism, or individualism.

Möller cultivated several lichens on media without the algal hosts, both from spores and from spermatia. With *Calicium pareitinum*, he produced several successive generations from the spermatia produced in spermagones in his cultures. His results demonstrate that lichens grow about as well on media as do most other fungi, the spermagones developing in five or six weeks. Bornet grew several lichens from widely separate families on their various algal hosts and demonstrated abundantly that lichen spores will attack these algæ and produce thalli. He often found the free algæ growing with others of the same species parasitised by lichens; and there is no reason to suppose that the spores do not germinate in nature, parasitize algæ and produce fully mature lichens commonly enough. Treub used wild *Chlorococcum* and also specimens of the same parasitized by several lichens, and found that the lichens all grew quite as well with the wild algæ as with those secured from lichen thalli. This and other similar results should forever refute the common statement that lichens do not often attack wild algæ, especially when we consider also that lichens probably almost always grow in proximity with the cosmopolitan terrestrial algæ which so commonly are their algal hosts. Möller sowed the alga, *Chroococcus*, on lobes of the *Thelephoric* ancestor of *Cora* and got the lichen *Cora*. By letting his cultures run for three or four years, Bonnier got several lichens to produce not only the sexual organs, but the apothecia as well. Had Möller used lichens like *Endocarpon pucillum* or *Polyblastia rugulosa*, which are known to produce both sexual organs and apothecia in two or three months when grown with the algal hosts, very probably he might have succeeded in getting the apothecia as well as the sexual organs in his cultures. If there is any doubt in the minds of those who read whether the lichen should be considered a fungus pure and simple rather than a dual organism, behaviour like that of other fungi in cultures with and without the host should be conclusive evidence, especially when the last doubt about lichen spores attacking wild algæ is removed.

Tobler has recently cultivated *Xanthoria parietina* both with and without the algal host on beerwort-gelatine. Calcium oxalate was stored in the lichen tissues when growing alone, but not when growing with the host. Artari has grown *Chlorococcum humicola*, obtained from lichen thalli, on organic media and obtained luxuriant growth and dark green color, though the alga was grown in absolute darkness or in light with CO₂ excluded. On media containing mineral salts but no organic matter, the algæ did not grow so well. Treboux more recently made similar cultures of about forty algæ and found that approximately half of them can secure carbon from media containing organic acids in the dark. He concluded that there is no sharp distinction between fungi and these algæ with respect to carbon assimilation. If some one could devise a way to ascertain whether algæ obtain the bulk of their carbon from the substratum in their natural habitats as they do in cultures, the problem would be solved, and we could conclude whether the lichen carries most of the food for the alga growing within it. But it seems probable that the method of nutrition of algæ in nature is more like that of higher green plants. Hence it seems doubtful whether the lichen carries much food to the algal host. This view will be strengthened further when we come to consider the relation of the lichen to the substratum.

Breathing pores have been postulated for lichens, and various crude openings in lichen thalli may be readily observed. These are non-corticate ventral surfaces of thalli, thin cortices at growing points, thin places with openings on upper surfaces of thalli, cracks in thalli, soralia, soredia, cyphellæ, empty spermagones, isidioid branchlets, and hollow cylinders in the centres of fruticose thalli. The last are often in contact with the exterior through dying away of the basal portions of the branch. Zukal believed that such crude makeshifts could serve for effective and sufficient æration of the algal hosts within lichens; but this can scarcely be possible, and the alga is doubtless placed in a disadvantageous position in lichen thalli with respect to æration, and may be forced to obtain its carbon in part through the lichen hyphæ from the substratum. We have taken pains to confirm Zukal's results by placing crustose thalli and sections of higher lichens under glycerine to prove the presence of

air along certain lines and in certain spots, but have not noted any pronounced air movements. The æration may suffice for the respiration of the lichen and its host, but is hardly sufficient for photosynthesis in the latter. Fünfstück, Schneider, Rosendahl, Jumelle, and Zopf have all worked on this problem, but have added little to what is stated above.

In spite of all hypotheses to the contrary, the lichen seems to bear a peculiar parasitic relationship to the alga. It is this modified condition of parasitism, in which the host is unicellular or filamentous and is usually surrounded and raised from the substratum by the parasite, that has obscured the relationship of the lichen parasite to its algal host. Lichen haustoria withdraw from the algal cells food elaborated for their own use, while the algæ are placed in a disadvantageous position with reference to light and air and are carried away from the substratum and imprisoned. The fact that the lichen may carry some food to the alga does not make good the disadvantages sustained by the latter. Elenkin, by staining carefully, found that the dead algæ in many lichens examined exceed the living in number, especially in the algal zone. He thinks that the lichen secretes an enzyme which kills the algæ, which are afterwards devoured saprophytically by the parasite, and has proposed the hypothesis of endosaprophytism to account for his results. His studies prove that the lichen is either parasitic or saprophytic on the alga, perhaps partly one and partly the other. Danilov finds that as lichen hyphæ enter the algal protoplasts they break up into delicate networks which penetrate through the protoplasts in various directions. The walls of these delicate hyphæ are very thin, and food is therefore the more readily absorbed from the protoplast. The algæ become pale and die through parasitism of the lichen. The researches of Elenkin and Danilov have perhaps done more to break down the consortium hypothesis than any other, though that of Peirce is also important.

Several workers have divided fresh water algæ into peptone and non-peptone assimilating algæ, but the recent work of Treboux indicates that if any algæ may be regarded as peptone algæ when growing in lichen thalli or in cultures, these same algæ are not such when living free. Then, if the method of nutrition is changed

when the alga is parasitized by a lichen, the change comes about quickly instead of requiring a long time as has been supposed by those who have overlooked the fact that parasitization of free algæ by lichens is common.

The relation of the lichen to its algal host cannot be understood until we know much more about that of the lichen to the substratum. Passing over the work of Schwendener, Frank and Lotsy, we may consider that of Lindau, who finds that lichen hyphæ do not penetrate into periderm cells, but spread out between them and force them apart. The dissolving of periderm cells is not sufficient to detect with the microscope, but nourishment must be secured from these cells; for *Ascomycetes* which do not parasitize algæ live in periderm as well as those that do, and these must secure nourishment. We venture to assert that hypophœodal lichens secure more nourishment from the periderm cells and little from the algal host with which they are not closely related. Crustose epiphœodal lichens are more closely related to their algal hosts and less closely with the substratum, and foliose and fruticose lichens penetrate but slightly into the periderm, while their relation with the algal hosts is more intimate. Thus the parasitism of the lichen upon the alga becomes more intense as we ascend the scale of development of these fungi.

Winter, Zukal, Bachmann, Fünfstück, Lang, Friederich, and Stahlecker have done telling work on the relation of certain lichens to the rock on which they grow, but the results are conflicting and uncertain. In general, it seems that lichens or their algal hosts act chemically on all rocks through substances secreted, affecting basic more than acid rocks. Here again, just in proportion as the lichen penetrates into the substratum, does it seem to depend less upon the algal host, which is then not so abundantly present. The role of fat abstraction from carbonate-containing rocks needs further study in spite of several lengthy papers, but Fünfstück found that some lichens can be made to live for years in rocks without their algal hosts.

Those who wish for a minute consideration of this subject are referred to the writer's paper in *Mycologia* for May, 1913.

SUMMARY AND CONCLUSION

1. Lichens often, and we believe usually, grow where the algal host lives free; and lichen spores are known to attack the algæ in nature as well as in cultures, just as the spores of other parasitic fungi attack their hosts.

2. Some lichens grow for months or for years in bark or rocks outside the relationship with the algal host. Also many families and genera of fungi contain some species which are lichens and others which are not, i. e. some species which grow with algæ and others which do not.

3. Lichens seem to grow as well on wild algæ as on those previously parasitized.

4. The alga is in a disadvantageous position in the lichen thallus with reference to carbon assimilation, respiration and light, and is killed by the lichen parasite.

5. The lichen receives more or less nourishment from the substratum;—all of it in certain low forms which live in the substratum, while growing outside the parasitic relation with the algal host, doubtless much of it in these after entering upon that relationship; less in other low crustose form that live partly or wholly on the substratum and sustain a closer relation with the more abundantly present algal host; still less in higher foliose and fruticose lichens.

6. The conditions of parasitism are peculiar in lichens on account of the internal host and the partial dependence on the substratum; but the points given above, in summarizing, prove conclusively that the lichen is a fungus pure and simple.

7. *Therefore, the lichen may be regarded as a fungus which lives during all or part of its life in parasitic relation with an alga and also sustains a relationship with some substratum such as bark, old wood, soil, rocks or stones, in which or on which it grows.*

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